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**Table 1. Viruses that are known or suspected to use ribosomal frameshifting**

<b>Animal viruses</b>	
<b>Retroviruses</b> (almost all retroviruses use programmed -1 ribosomal frameshifting)	
Lentiviruses (immunodeficiency viruses, IVs)	Human HIV1 and HIV2, simian SIV (including many species-specific viruses), feline IV, bovine IV, Visna virus (sheep), arthritis-encephalitis virus of goats, equine infectious-anaemia virus.
T-cell lymphotropic viruses (xTLVs)	Human HTLV I and II, simian STLVs, bovine LV
Avian leukosis viruses	Leukaemia and sarcoma viruses of many birds, e.g. Rous sarcoma virus
Type-B retroviruses	Includes mouse-mammary-tumour virus
Type-D Retroviruses	Mostly characterized in monkeys and sheep; includes Mason-Pfizer monkey virus and ovine pulmonary adenocarcinoma virus
<b>Nidoviruses</b>	(Genera <i>Coronavirus</i> , <i>Torovirus</i> and <i>Arterivirus</i> )
Human coronaviruses	229E, OC43, etc. Common cold, upper-respiratory-tract infections, pneumonia, gastroenteritis
Human toroviruses	Enteric and respiratory diseases
Animal coronaviruses	Calf coronavirus
Animal toroviruses	Breda virus (calves); bovine respiratory virus, Berne virus (horses), porcine torovirus, feline torovirus
Animal arteriviruses	Simian haemorrhagic-fever virus, equine arteritis virus, Ixistad virus (porcine reproductive and respiratory syndrome virus); VR2332 virus (pigs), lactate-dehydrogenase-elevating virus (rodents)
<b>Paramyxoviruses</b>	-1 ribosomal frameshifting reported in measles
<b>Astroviruses</b>	Human astroviruses 1-5; bovine; ovine; porcine; canine; duck
<b>Plant viruses</b>	
<b>Tetraviruses</b>	
Sobemoviruses	e.g. Southern-bean mosaic virus; cocksfoot mottle virus
Leuteoviruses	e.g. Barley yellowdwarf virus; beet western yellows virus; potato leaf roll virus
Enamoviruses	e.g. Pea enation mosaic virus
Umbraviruses	e.g. Carrot mottle virus
<b>Tombusviruses</b>	
Tombusvirus	Tomato bushy stunt virus
Carmovirus	Carnation mottle virus
Necrovirus	Tobacco necrosis virus
Dianthoviruses	Red-clover necrotic mosaic virus
Machlomovirus	Maize chlorotic mottle virus
<b>Totiviruses</b>	L-A and L-BC (yeast); related viruses of other fungi?
	<i>Giardia lamblia</i> virus (intestinal parasite)
	<i>Triconella vaginella</i> virus (human parasite)
	<i>Leishmania brasiliensis</i> virus (human parasite)
	Other viruses of protozoa?
<b>Bacteriophages</b>	
<b>Podoviruses</b>	T7 phage
<b>Siphoviruses</b>	$\lambda$ -Phage group

positioning of the spaces], where XXX can be any three identical nucleotides, YYY can be AAA or UUU, and Z is A, U or C (Fig. 3)<sup>10,18-20</sup>. The second promoting element is usually a sequence that forms a defined RNA secondary structure, such as an RNA pseudoknot, approximately six nucleotides 3' of the slippery site and is thought to increase the probability that the ribosome will slip reading frame in the -1 direction (Fig. 3)<sup>21,22</sup>. The simultaneous slippage of both ribosome-bound tRNAs by one base in the 5' direction still leaves their non-wobble bases correctly paired with the mRNA in the new reading frame (Fig. 3). Thus, the number of ribosomes that shift frame is affected by a number of parameters, including the ability of the ribosome-bound tRNAs to unpair from the 0-frame, the ability of these tRNAs to rebind to the -1 frame, the relative position of the RNA

pseudoknot from the slippery site and the pseudoknot's thermodynamic stability<sup>10,19,20,23-28</sup>.

#### Advantages of targeting programmed frameshifting

The fact that programmed -1 ribosomal frameshifting appears to be virus specific makes it an attractive target to identify agents that affect the efficiency of this process and, consequently, of virus maintenance. We can envisage three major advantages to programmed -1 ribosomal frameshifting as a therapeutic target for antiviral agents.

(1) Small changes in frameshifting efficiencies can have large effects on virus production; for example, increasing or decreasing the efficiency of programmed -1 ribosomal frameshifting by the yeast L-A virus by as little as a factor of two interfered with the ability of